

FEEDING ACTIVITY IN *ECHINASTER* AND ITS INDUCTION WITH DISSOLVED NUTRIENTS¹

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While many species of starfishes are notorious for their predaceous attacks on edible shellfish, others, particularly those belonging to the family Echinasteridae, have been considered economically harmless. Indeed, until fairly recently we remained almost completely ignorant of the normal food habits and nutritional mechanisms of this latter group of animals. In 1960, Anderson published the first truly accurate and detailed account of the histology and structure of the digestive system of a member of this family, *Henricia leviuscula*. He also presented a reasonable analysis of the functioning of this system in the collection and processing of nutritive materials. Particularly, he called attention to the fact that the Tiedemann's pouch, a conspicuously developed outgrowth of the pyloric stomach found beneath each digestive gland, acts as "a hydrodynamic organ or flagellary pump of prodigious effectiveness" (p. 393). These structures transport material from the flagellary tracts of the stomach and rapidly distribute it to secretory and absorptive areas in the digestive glands, maintaining it in continuous circulation through these organs "until digested, absorbed, or eliminated" (p. 392). To support the hypothesis that *Henricia* is primarily a particulate feeder, Anderson exposed two specimens of *Henricia sanguinolenta* to suspensions of dyed *Mytilus* sperm. These were seen to be drawn up into the partially opened mouth of the starfish, collected as streams in the radial peristomial grooves, or entangled in strands of mucus that also moved into the mouth. The dyed food particles were subsequently found at various places in the Tiedemann's pouches.

While Anderson pointed out that, in feeding, the cardiac stomach of *Henricia* probably could not be everted to the extent of the stomachs of such starfishes as *Asterias* and *Patiria*, he did note that in some specimens stomach vesicles press through the mouth as lobe-like structures extending about a millimeter. The extension of the stomach as a button-like protuberance has been seen by a number of other investigators, including the author. Vasserot (1961) notes this ability in both *Henricia sanguinolenta* and *Echinaster sepositus*. In fact, he concludes that these two species are primarily macrophagous feeders restricted almost exclusively to a diet of sponges, or are at least stimulated to assume a feeding posture by sponge fragments.

In further studies on *Henricia sanguinolenta*, Rasmussen (1965) has confirmed Anderson's opinion that this species is primarily a filter feeder, capable of removing diatoms and flagellates from suspensions at high rates. He concludes that Vasserot misinterpreted his observation in that *Henricia*, even when mounted on a sponge, was not significantly harming it, but rather benefiting from the sponge's water

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currents while functioning as a suspension feeder. He refers to this relationship as a state of "energy commensalism" (p. 187).

Other evidence is available that neither particle-suspension nor macrophagous feeding fully explain the nutrition of these starfishes. Stephens and Schinske (1961) first noted that *Henricia sanguinolenta* (along with many other invertebrates) could take up dissolved glycine from sea water. Ferguson (1963, 1967a, 1967b, 1968b) has since explored in much greater detail uptake from dilute solutions of free amino acids and sugars by starfish. Ferguson has emphasized that these substances may significantly contribute to the maintenance of the superficial tissues of the body, which otherwise might have difficulty obtaining sufficient nutrients from internal sources.

While in Ferguson's experiments, free dissolved nutrients were generally not taken into the digestive system and deeper regions of the body, several instances of such uptake were noted in both *Henricia sanguinolenta* and *Echinaster echinophorus*. These instances occurred sporadically when specimens of these species were exposed to fairly high concentrations of glucose. They indicate the possibility that completely dissolved nutrients, when present in sufficient concentration, can stimulate the filter pumping machinery of the organisms into operation. The observation of such a response is most interesting in that it could be interpreted as showing that filter-pumping by starfish is a significant function in a variety of nutritional roles, including the uptake not only of suspended material, but also of dissolved substances from different sources. These substances could be obtained from external digestion, decaying (or autolyzing) carrion and detritus, or simply organically rich sea water. The present study was carried out in order to provide further information on the feeding behavior of *Echinaster echinophorus* and to more fully delineate the ability of dissolved nutrients to stimulate filter-pumping in this species.

MATERIALS AND METHODS

In addition to collecting observational data on the normal feeding habits of the Echinasteridae, experimental evidence was sought to more clearly define the nutritional capabilities of these starfish. The primary approach used in these experiments was to expose animals to various concentrations of different dissolved nutrients to permit determination of the adequate stimuli for inducing them to engage in the filter-pumping "feeding" process. As neither the method of Anderson (1960), involving direct observation of the ingestion of particles, nor that of Rasmussen (1965) involving colorimetric observation on food organism cultures exposed to the starfish, appeared to be suitable for determining whether the experimental animals had engaged in filter-pumping during an experimental period, another procedure had to be devised. The method finally chosen was a simplified, essentially qualitative version of that previously used in nutrient utilization studies (Ferguson, 1967a).

Starfish, *Echinaster echinophorus*, were collected from tidal grass flats and kept on a sea table in recirculating water for several days. (Specimens were examined by Maureen Downey of the U. S. National Museum and tentatively assigned by her to this species, pending revision of the group. In previous papers by the author the same form has been referred to as *Echinaster spinulosus*.) Only mod-

erate size individuals were selected for further study. As the experiments were all performed during the midsummer period, the gonads of these specimens were in a relatively early stage of redevelopment from the spring spawning, and the digestive glands occupied most of the coelomic cavity. Pairs of specimens were placed together in finger bowls containing 100 ml of filtered sea water from the same sea table, to which had been added a carefully measured quantity of the nutritive substance under investigation, and a small quantity of high specific activity C^{14} -labeled nutrient. No attempt was made to accurately measure the latter, as it contributed negligible mass, and the variety of labeled substances used were obtained from several sources of different strengths. The only concern was that sufficient labeled marker was present to be easily detected in the samples if the nutrients were taken up. The initial high purity of both the labeled and unlabeled compounds was verified from data provided by the manufacturers, and all the compounds were stored under optimum conditions to maintain stability.

Each experiment was allowed to continue for 4 hours. Following this period the animals were removed from the bowls, rinsed in 3 changes of sea water, and dissected into two parts—the digestive glands (including the Tiedemann's pouches) and the remaining structures (chiefly body wall). Each of these was then placed in a test tube together with 1 ml of 10 per cent NaOH. After dissolving the tissues by heating the test tubes in boiling water for a few minutes, the resulting digests were decanted into 1-inch steel planchets, dried overnight in an oven, and counted as "infinitely thick" samples in an automatic G-M counter. The data were evaluated subjectively, primarily by comparing the level of radioactivity found in the digestive glands with that found in the body wall of each specimen.

A list of the nutrients tested may be found in Tables I and III. Each of the compounds listed in Table I was used in conjunction with its uniformly C^{14} -labeled counterpart. In Table III, lactalbumin hydrolysate was used as a representative mixture of amino acids. Its uptake was tested with a commercial mixture of uniformly labeled C^{14} -amino acids (representing a synthetic algal protein hydrolysate) obtained from New England Nuclear Corp., Boston, Mass. As examples of proteins, gelatin, casein, and bovine serum albumin were tested with a purified algal protein- C^{14} , also obtained from New England Nuclear Corp.

OBSERVATIONS

General observations on feeding

As was noted by Vasserot (1961), *Echinaster* is often found in the field in association with sponges. In the present collections of 1136 specimens, 369 (32.5%) were found in such associations, and with their stomachs partially everted. In some cases the sponges showed signs of damage, but generally they were still quite healthy. The relationship with sponges does not appear to be exclusive, however, as in the same collections 44 specimens (3.7%) were found in a feeding position on detritus-rich sand, 23 (2.0%) on algae, 21 (1.9%) on ascidians, 16 (1.4%) on snails, and 1 on an annelid. The remaining 662 (58.3%) showed no evidence of feeding activity, and often appeared to be in transit across the substrate. In captivity, specimens will readily settle in a feeding position on shellfish which have been opened for them (Fig. 1). They will also frequently attack more defenseless species, such as sunray clams (*Macrocallista*) and sand dollars

(*Mellita*). While victims of such attacks often show signs of being damaged by digestive activity, they are practically never completely devoured. Rather, the remains are abandoned after about 24 hours.

In practically all cases when a captive specimen is seen in a feeding posture, its stomach is found to be everted as a distinctive button-like structure. Such eversion was also noted in many of the experiments with soluble nutrients (Fig. 2). Almost invariably, when eversion was seen in the experiments, significant radioactivity was later located in the digestive glands. In many cases, however, radioactivity was found in the digestive glands of specimens which were not observed with everted stomachs. It is quite possible that in these cases brief periods of eversion may have been overlooked.

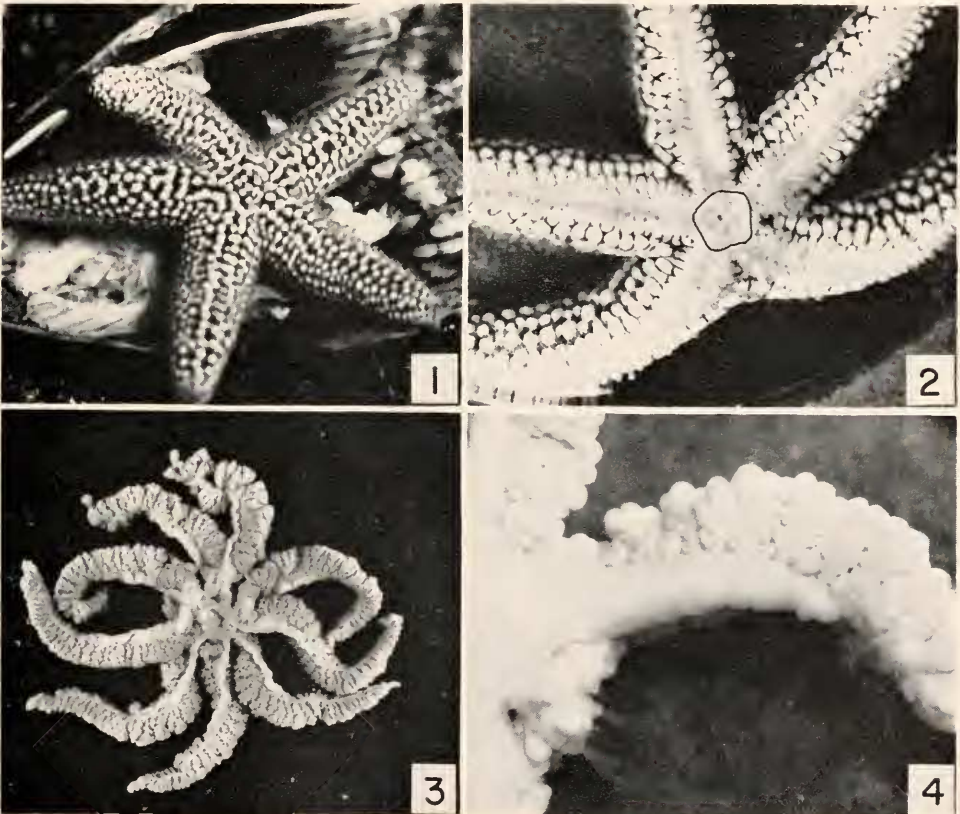


FIGURE 1. *Echinaster* in a typical feeding position on an opened pen shell clam (*Atrina*).

FIGURE 2. Oral view of *Echinaster* with everted stomach (outlined). Eversion was induced by placing the animal in 100 mg % lactalbumin hydrolysate.

FIGURE 3. Oral view of dissected digestive system of *Echinaster*. Mouth and small pyloric stomach may be seen in center. Note that the Tiedemann's pouch extends for $\frac{1}{3}$ to $\frac{1}{2}$ the length of each digestive gland.

FIGURE 4. Detail of Tiedemann's pouch showing its attachment to the digestive gland and the pyloric stomach.

Anatomy and histology

Dissection and routine histological study reveal that the digestive system of *Echinaster* is very similar to that described for *Henricia* by Anderson (1960). Each digestive gland is attached to the pyloric stomach by a well-developed Tiedemann's pouch (Figs. 3 and 4). The pouch is divided into a series of diagonal channels by "seam-cell" adhesion-bands. These channels are very heavily lined with cilia (flagella), and doubtless do form a very powerful pumping organ. As in *Henricia*, the epidermal nerve plexus and associated "spindle nerve cells" are very well developed in the floor of the Tiedemann's pouch, along the adhesion-bands, and along the line of attachment of the Tiedemann pouch and the digestive gland.

TABLE I

Relative uptake of dissolved labeled nutrients by body wall and digestive glands

Nutrient	CPM $\left(\frac{\text{Digestive glands}}{\text{Body wall}} \right)$											
	Concentration 1.0 mM				2.5 mM				5.0 mM			
Glycine	$\frac{34}{966}$	$\frac{350}{991}$	$\frac{17}{411}$	$\frac{143}{431}$	$\frac{73}{1375}$	$\frac{102}{1352}$	$\frac{17}{1543}$	$\frac{616}{2120}$	$\frac{500}{3320}$	$\frac{948}{3320}$	$\frac{315}{262}$	$\frac{225}{259}$
L-alanine	$\frac{7}{285}$	$\frac{11}{393}$	$\frac{14}{195}$	$\frac{11}{218}$	$\frac{60}{93}$	$\frac{36}{74}$	$\frac{43}{863}$	$\frac{28}{721}$	$\frac{410}{1984}$	$\frac{1069}{1415}$	$\frac{9}{82}$	$\frac{52}{88}$
L-serine					$\frac{42}{776}$	$\frac{85}{638}$			$\frac{81}{1149}$	$\frac{184}{1177}$		
L-valine	$\frac{22}{683}$	$\frac{27}{729}$	$\frac{77}{734}$	$\frac{42}{580}$	$\frac{16}{668}$	$\frac{37}{500}$	$\frac{42}{442}$	$\frac{46}{488}$	$\frac{509}{338}$	$\frac{20}{363}$	$\frac{61}{304}$	$\frac{68}{388}$
L-leucine	$\frac{93}{961}$	$\frac{866}{1233}$	$\frac{42}{974}$	$\frac{11}{1039}$	$\frac{141}{642}$	$\frac{348}{700}$	$\frac{1074}{311}$	$\frac{251}{350}$	$\frac{334}{848}$	$\frac{140}{581}$	$\frac{295}{499}$	$\frac{1889}{514}$
L-isoleucine	$\frac{10}{145}$	$\frac{31}{200}$	$\frac{25}{391}$	$\frac{90}{586}$	$\frac{43}{160}$	$\frac{8}{180}$	$\frac{72}{511}$	$\frac{65}{346}$	$\frac{219}{150}$	$\frac{123}{99}$	$\frac{302}{288}$	$\frac{42}{340}$
L-phenylalanine	$\frac{505}{661}$	$\frac{217}{798}$	$\frac{445}{179}$	$\frac{391}{161}$	$\frac{988}{533}$	$\frac{53}{364}$	$\frac{312}{109}$	$\frac{1227}{83}$	$\frac{1258}{407}$	$\frac{1062}{372}$	$\frac{294}{58}$	$\frac{273}{56}$
L-arginine	$\frac{8}{298}$	$\frac{10}{225}$	$\frac{4}{177}$	$\frac{7}{216}$	$\frac{8}{186}$	$\frac{9}{198}$	$\frac{17}{254}$	$\frac{11}{187}$	$\frac{10}{188}$	$\frac{7}{125}$	$\frac{9}{165}$	$\frac{8}{146}$
L-lysine					$\frac{48}{358}$	$\frac{10}{236}$	$\frac{49}{522}$	$\frac{120}{499}$	$\frac{23}{491}$	$\frac{16}{399}$	$\frac{66}{415}$	$\frac{9}{383}$
L-glutamic acid	$\frac{10}{235}$	$\frac{6}{145}$	$\frac{6}{114}$	$\frac{5}{90}$	$\frac{257}{1148}$	$\frac{89}{1229}$	$\frac{14}{165}$	$\frac{13}{147}$				
D-glucose	$\frac{15}{282}$	$\frac{427}{277}$	$\frac{55}{249}$	$\frac{33}{161}$	$\frac{3120}{286}$	$\frac{7057}{748}$	$\frac{2223}{248}$	$\frac{561}{247}$	$\frac{204}{892}$	$\frac{2185}{250}$	$\frac{1990}{327}$	$\frac{1426}{329}$

These nervous elements may be very significant in controlling the pumping activity of the pouch.

Pumping and the uptake of soluble nutrients

When the starfish were exposed to various concentrations of soluble nutrients, very distinctive patterns of response were noted (Tables I, II, III). In essentially all cases the body wall (epidermis) took up observable quantities of the nutrients. Such a result was expected from previous experiments (Ferguson, 1963, 1967a, 1967b, 1968b), although this represents the first time that the epidermal uptake of many of the specific compounds has been confirmed. Varying degrees of radioactivity were also found in the digestive glands. Some of this was doubtless due to unavoidable contamination during the dissection of the organs from the animal;

TABLE II
Feeding interpretation of experiments listed in Table I

	Concentration 1.0 mM	2.5 mM	5.0 mM
Glycine	- (+) - (+)	- - - (+)	- (+) + +
L-alanine	- - - -	+ + - -	(+) + - +
L-serine		- -	- -
L-valine	- - - -	- - - -	+ - (+) -
L-leucine	- + - -	(+) + + +	+ (+) + +
L-isoleucine	- - - -	(+) - - -	+ + + -
L-phenylalanine	+ - (+) -	+ - + +	+ + + +
L-arginine	- - - -	- - - -	- - - -
L-lysine		- - - -	- - - (+)
L-glutamic acid	- - - -	(+) - - -	
D-glucose	- + (+)(+)	+ + + +	+ + + +

Each mark represents the behavior of a separate specimen: - = insignificant amount of feeding activity; (+) = possibly significant amount of feeding activity; + = probably significant amount of feeding activity.

most of the remainder probably reached the organs in intervals of ciliary pumping by the Tiedemann's pouches during the 4-hour exposure period. In extreme cases, where ciliary pumping apparently persisted over most of the exposure period resulting in a large percentage uptake by the digestive glands, a markedly lower incorporation could be noted in the body wall, doubtless because less activity remained in the media to be taken up by these elements. Likewise, when very high concentrations of nutrients were present, reduced uptake of tracer was observed in all parts—probably due to the saturation of the absorptive mechanisms. This phenomenon is most noticeable in Table III with the higher concentrations of lactalbumin hydrolysate.

In light of the aforementioned variables—possible contamination of tissue samples, individual variations in the duration of the pumping, and competitive inhibition of uptake—arbitrary criteria had to be established to simplify the task of interpreting

TABLE III
*Relative uptake of dissolved labeled nutrients by body wall and digestive
glands and interpretation*

Nutrient	Concentration mg%	CPM ($\frac{\text{Digestive glands}}{\text{Body wall}}$)				Feeding interpretation*
Amino acid-C ¹⁴ mixutre & Lactalbumin hydrolysate	0	288 9788	197 11846	40 3832	69 3583	- - - -
	10	84 4807	130 4348	26 1022	833 1022	- - - +
	25	347 608	2378 567			+ +
	50	596 627	4818 701			+ +
	75	680 635	3016 566			+ +
	100	92 1472	1302 1135	2765 588	374 425	- + + +
	125	1986 474	1302 401			+ +
	150	921 327	1302 401			+ +
	500	51 223	58 205			(+)(+)
	1000	69 179	105 240			(+)(+)
Algal Protein-C ¹⁴ & Gelatin	10	30 142	34 314	24 173	20 179	(+) - - -
	50	63 156	28 146	63 105	24 150	+ - + -
Algal Protein-C ¹⁴ & Casein	10	28 412	40 101	22 93	864 120	- (+) - +
	50	26 48	41 59	60 130	38 70	+ + + +
Algal Protein-C ¹⁴ & Serum Albumin	10	30 294	20 258	23 289	18 219	- - - -
	50	29 277	14 275	15 180	16 232	- - - -
Algal Protein-C ¹⁴ alone	(Negligible)	43 311	45 255	23 213	554 513	- - - +

* See Table II for clarification of symbols.

the experimental results. Therefore, when the level of radioactivity found in the digestive glands was over 40% of that found in the body wall, a significant degree of pumping (feeding) was considered to have probably occurred. Less than 20% was considered insufficient evidence for feeding, while 20–40% was considered as possibly significant feeding activity. These interpretations are presented in Tables II and III. On this basis, very marked differences in the stimulating effects of different substances may be noted.

DISCUSSION

There can be little doubt that these starfish are capable of making effective use of a great variety of soluble materials, absorbing them not only into their exposed epidermal tissues, but also, actively pumping them up and assimilating them into their internal digestive organs. A measure of the efficiency of the latter process can be seen in the observation (Table I) that some of the glucose-exposed specimens took up as much as 10 times the dissolved nutrient internally as they did into the exposed superficial tissues.

In most cases, however, much smaller ratios of uptake between the two areas are apparent. Some "background" activity is, of course, always found in the digestive glands. This usually amounted to several per cent of the activity found in the body wall and (as previously stated) was probably due to unavoidable contamination of the samples and other causes. But beyond this low level, considerable variation exists in the uptake of nutrients into the digestive glands even of specimens exposed to the same conditions (Tables II and III). Thus, it seems likely that the individual specimens have considerable control over their activities. They do not pump up material continually, but take it up over periods of varying lengths of time. The ingestion appears to be a relatively high order response on the part of the animals, and not a simple reflex activity entrained to a minimal adequate stimulus.

The ability of starfish to limit ciliary pumping to periods when it might be most productive in obtaining nutrients would, of course, be a significant advantage to them in terms of conservation of energy. It is quite clear from Tables II and III that higher concentrations of dissolved nutrients are generally much more successful than lower ones in stimulating pumping. Thus, concentrations of 25 mg% or greater of mixed amino acids (Table III) almost invariably induce significant uptake, while only one animal in four responded positively to a concentration of 10 mg%. When one considers the energy that would be required to pump up the water through the narrow digestive channels and extract the dissolved nutrients from it, it is doubtful that concentrations of nutrients much below this order of magnitude could be utilized at a net energy gain. Very much lower concentrations of soluble nutrients are taken up by the superficial tissues, however, where the animal could rely almost entirely on the natural circulation of the environmental fluids and would need expend energy only for the active transport process (Ferguson, 1967a, 1967b).

Not all the compounds tested were equal in their ability to stimulate pumping. Glucose apparently is a most efficient stimulus, being very effective even at a concentration of 1.0 mM (Table II). It is not surprising, then, that it was with this compound that the pumping reaction was first evoked in *Henricia* (Ferguson, 1967a). Most of the neutral amino acids appear to be moderate stimulators,

although a good deal of variation exists between them. Leucine and phenylalanine were particularly efficient, while no positive response at all was obtained in the four experiments with serine. The other neutral amino acids gave rather mixed results. The basic amino acids, arginine and lysine, and the acidic glutamic acid produced very little evidence of pumping activity.

Special note should be made of the results obtained with glutamic acid. Although it is relatively limited in its solubility, this amino acid has proven to have a number of interesting and as yet unexplained properties in echinoderm physiology. In previous experiments with *Echinaster*, for example, it appeared to enhance the serosal transport of other amino acids into the digestive glands, in spite of its own modest rate of transport (Ferguson, 1968a). It also produced both stimulatory and inhibitory effects on the muscle tone of these organs (Ferguson, 1966). In extracts of digestive glands and ovaries it is one of the few amino acids consistently present (Ferguson, unpublished). In *Asterina* it has been implicated as an inhibitor of a spawning substance obtained from the radial nerves (Ikegami, Tamura, and Kanatani, 1967). In light of these findings, one might expect glutamic acid to play at least some role in controlling the nutritional activities of these species. Thus, even the present essentially negative findings may prove to have significance as more information is obtained.

While many simple, low-molecular weight substances are apparently sought and taken up by starfishes, there is great uncertainty about the role of large molecules, particularly proteins, in this regard. One would, of course, expect predaceous species, such as *Asterias* and *Pisaster*, to take up these substances in conjunction with their well-known feeding habit of digesting bivalves in their shells. The only modern account of direct evidence for the uptake of soluble protein by a starfish is provided by Araki (1964), who notes that the everted stomach of *Patiria* will take up albumin. While this species possesses a Tiedemann's pouch system, it apparently is much less efficient than that found in the Echinasteridae (Anderson, 1960). This starfish feeds by extruding its enormous stomach over the sea bottom and devouring whatever is covered.

If *Echinaster* can respond so effectively to low-molecular weight amino acids and sugars, it would seem likely that it would also respond positively to dissolved proteins. The experiments which were carried out to verify this fact, however, were not fully successful.

The algal protein-C¹⁴ used as a label in these experiments was a highly purified product, but was only sparingly soluble in sea water. After its use, significant levels of radioactivity were found in the body wall (and in some cases the digestive glands) of animals exposed to it, but this activity could have been picked up in other ways. For example, it may represent protein simply adsorbed on the body surface, or the uptake of amino acid obtained from the breakdown of the labeled protein. Such breakdown could be due to the action of the well-developed secretory glands found in the epidermis, although no enzymatic activity has yet been observed in the products of these glands. Enzymes could also be released into the medium via the mouth. Bacterial decomposition of the protein during the four-hour experimental period is also a possibility.

In spite of these problems, some tentative conclusions can still be reached from the data obtained (Table III). None of the proteins tested, for example, appeared

to be as effective in stimulating feeding as did the equivalent amount of free amino acid. Most of the positive reactions recorded were in reality minimal effects. Only in two of the twenty-eight experiments did greater amounts of radioactivity become localized in the digestive organs than in the body wall. And even in one of these two cases the positive results were obtained without the benefit of additional proteins added to the algal- C^{14} solution. These two cases, however, do indicate fairly clearly that at least in some circumstances free proteins can be removed from sea water and utilized by this species.

In summary, the current study demonstrates that *Echinaster*, like *Henricia*, possesses an efficient pumping mechanism. These animals can be stimulated to turn on this pump by the presence of free amino acids, glucose, and possibly protein in their surrounding medium, and can efficiently take up and absorb soluble compounds into their internal digestive organs. While this process is an intermittent one, generally requiring certain minimal concentrations of the dissolved nutrients, these same nutrients may be continually absorbed by the superficial tissues, even from extremely dilute solutions.

Furthermore, behavioral characteristics of the species serve to greatly enhance the possibility of obtaining such soluble nutrients. While the often-seen association of *Echinaster* with sponges might indeed represent "energy commensalism," it may well also represent a form of parasitism. The everted stomach may release enzymes which would act to produce low molecular products in a very localized region where they would be pumped up by the starfish. Loosely organized sponge tissues do not very readily show this damage, but such an effect is clearly evident as whitish splotches on sand dollars attached by this species in captivity. Such external enzymatic activity need only be of secondary importance, however, as the starfish can be equally efficient in picking up naturally released products and particulate materials. These might emanate from the bodies of sponges or from other soft-bodied invertebrates which may be attacked, or be obtained from carrion, detritus, or even organic-rich sea water.

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SUMMARY

1. *Echinaster echinophorus* possesses a digestive system very similar to that of *Henricia*. Its Tiedemann's pouches are well developed and appear to function as pump organs.

2. About one third of the specimens seen in the field are found in a feeding posture on sponges (even though the sponges do not appear to be greatly harmed). Occasionally specimens are also found with everted stomachs on sand, algae, ascidians, molluscs, and other organisms. Captive specimens will assume a feeding position on opened clams and other defenseless invertebrates, but rarely completely devour them.

3. Tracer experiments demonstrate that various dissolved amino acids, glucose, and possibly proteins are taken up continually by the exposed superficial tissues of

the body. If present in suitable concentration (usually about 25 mg%) most of these substances will also be taken up into the internal digestive organs, presumably because they stimulate the animals to engage in filter-pumping.

4. Of the substances that have been studied, glucose is the most effective stimulator of the pumping process, followed by the neutral amino acids (particularly leucine and phenylalanine). The charged amino acids—arginine, lysine, and glutamic acid—are very poor stimulators, as are apparently several types of protein.

5. It is concluded that the digestive apparatus of *Echinaster* can function effectively in collecting nutrients from a variety of sources. It can take up dissolved nutrients released through modest external digestive activity or obtained from other natural sources, such as carrion, detritus, or organic-rich sea water. It may also be able to accumulate considerable quantities of particulate materials.

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